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Ecophysiological drivers of hardwood plantation diameter growth under non-limiting light conditions

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ABSTRACT

While light is a primary driver of tree growth and development, other environmental variables are also essential, including water, nutrients, and temperature. Ecophysiological studies have helped to uncover mechanisms underlying these interactive processes, but such trials have been mainly conducted on seedlings, with relatively few dealing with trees past the sapling stage. We used environmental and ecophysiological data collected on 28 trees (age 14–20 years) across three study sites in Indiana, USA for several growing seasons to identify variables that drive diameter growth of plantation-grown hardwoods past the sapling stage under non-limiting light conditions. Results showed that water stress (as reflected in leaf water potential) had the greatest influence on growth; relative diameter growth of black walnut (*Juglans nigra* L.), northern red oak (*Quercus rubra* L.), and white oak (*Quercus alba* L.) was reduced with increasing water stress. Compared to previous studies carried out with seedlings, results provide some evidence to suggest that ecophysiological responses to water stress may differ between seedlings, juveniles, and mature trees of the same species. Relative diameter growth of black walnut and northern red oak increased with increasing soil or leaf nitrogen. We did not find relationships between relative diameter growth of white oak and nutrient variables. Overall, these results have important implications for reforestation and forest management efforts in light of climate change.

1. Introduction

Light is essential to tree growth as it drives photosynthesis, and the products of photosynthate can be allocated to several functions, including primary or secondary growth. Other environmental variables are also essential to tree growth, including water, nutrients, and temperature. Water stress, nutrient deficiencies, or heat stress can have substantial negative impacts on ecophysiological processes, leading to reduced growth or mortality. Ecophysiological studies are essential to gain a better understanding of these processes.

Consequently, the number of forestry ecophysiological studies has steadily increased over the past three decades, but these have been largely focused on seedlings (Fig. 1). Studies that deal with trees past the sapling stage represent about 10% of the total (Fig. 1), and this percentage has been stable over time. Even fewer studies attempted to link ecophysiological measurements of trees past the sapling stage with their corresponding growth responses under non-limiting light conditions. Further, the majority of studies that have addressed ecophysiology of mature trees in the last decade have been conducted on gymnosperms (70%), with relatively fewer in angiosperms (30%). Several deciduous angiosperms are highly desirable species, such as black walnut (*Juglans nigra* L.), northern red oak (*Quercus rubra* L.), and white oak (*Quercus alba* L.). Stands past the sapling stage enter a critical developmental period of stem exclusion that can last several decades, and where competition for resources leads to slow growth and/or mortality. Ecophysiological studies can determine if water, nutrient, and temperature stress at the seedling stage are still important past the sapling stage, and thus help to guide reforestation and forest management efforts.

Previous dendroecological and ecophysiological studies have shown that the three species differ in their responses to environmental stress. At one end of the spectrum, black walnut is a well-known desiccation avoider (Gauthier and Jacobs, 2011) and its susceptibility to water deficits has been documented at the seedling stage (Davies and Kozlowski, 1977; Parker and Pallardy, 1985; Ni and Pallardy, 1991). Black walnut is shade-intolerant and has a narrow range of soil conditions on which it grows well due to high nutrient and soil pH requirements (Thompson and McComb, 1962; Paschke et al., 1989; Ponder, 1998). At the other end of the spectrum, white oak is considered desiccation tolerant (Parker et al., 1982; Abrams, 1990). White oak is moderately shade tolerant, can grow well on a wide range of sites (e.g. Hutchinson et al., 1999), and grows best on xeric-mesic and mesic

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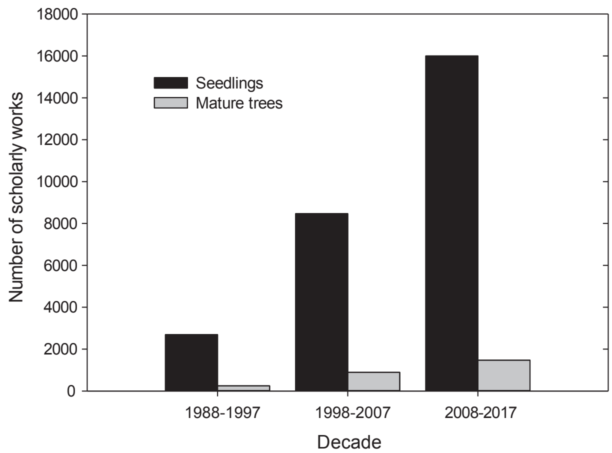

Fig. 1. Number of scholarly works published in the field of ecophysiology that dealt with either seedlings or mature trees over the past three decades. Source: Google Scholar, keyword search: "ecophysiology" and "seedlings"; "ecophysiology" and "mature trees". Accessed on 31 October 2017.

sites (Fralish, 2004). This suggests nutrient requirements are lower than for black walnut. Northern red oak is less sensitive to water stress than black walnut, but more sensitive than white oak (Hinckley et al., 1978, 1979; Bahari et al., 1985). Northern red oak is moderately shade tolerant, can also grow on a wide range of site conditions (Hutchinson et al., 1999), but is often considered to grow best on mesic sites (Fralish, 2004).

Numerous dendroecological studies have shown the influence of temperature on diameter growth rates of northern red oak and white oak (Abrams and Copenheaver, 1999; Rubino and McCarthy, 2000; van del Gevel et al., 2012). Ecophysiological studies have found that photosynthesis of northern red oak and white oak decreases with increasing leaf temperature (Hinckley et al., 1978). Oak may have greater photosynthetic capacity than walnut at high air temperatures in the 32–40 °C range (Dreyer et al., 2001). Soil temperature can have indirect and beneficial effects on growth via increases in nutrient availability or root production, as shown for hybrid walnut species (Contrador et al., 2015).

Thus, we used *in situ* ecophysiological data from three separate study sites to identify water, nutrient, and temperature variables that drive diameter growth of plantation-grown black walnut, northern red oak, and white oak under non-limiting light conditions. We hypothesized that water, nutrients, and temperature would all contribute based on their documented influence on deciduous angiosperms. We also hypothesized that water stress would be the most important limitation to growth across species, followed by nutrient stress, and temperature stress (Kozlowski and Pallardy, 1997).

2. Materials and methods

2.1. Study sites

Data for this study was collected from 2006 to 2008 on three separate hardwood plantations located in and around West Lafayette, Indiana, USA (Table 1). Mean annual temperature (1981–2010) for this area is 10.0 °C and mean annual precipitation is 991 mm (NCEI, 2017). The first study site was established in 1989 with 1 + 0 black walnut bareroot stock at a spacing of 6.8 m between rows and 1.5 m between trees. The site was composed of deep, well-drained Ockley silt loam on less than 2% slope. Thinning of lower-quality trees was performed yearly from 1990 until the beginning of the study. The landowner's objective was to maintain the crown competition factor near 100 based on guidelines for managing black walnut (Schlesinger and Funk, 1977). Corn (*Zea mays* L.) was grown between rows for the first 6 years after planting. Mean stand density at study initiation was ~375 trees ha^{-1} and mean basal area was ~15.0 m^2 ha^{-1}.

The second study site was established in 1994. Billett loam is the dominant soil type on this former agricultural land, characterized by well-drained soils on less than 2% slope. Black walnut, white oak, and northern red oak 1 + 0 bareroot seedlings, 30–45 cm in height at time of planting, were planted at 2.4 × 2.4 m spacing. Planting pattern was not consistent, i.e., species did not alternate evenly among or between rows. Mean stand density at study initiation was 1324 trees ha^{-1} and basal area was 10.8 m^2 ha^{-1}.

The third site was established in 1994 on former agricultural land, composed of Kalamazoo loam, characterized by well-drained soils formed in loamy outwash overlying sand or loamy sand (NRCS, 2007). Northern red oak, white oak, black walnut, and black cherry (*Prunus serotina* Ehrh.) 1 + 0 bareroot seedlings were planted at ratios of 2, 2, 3, and 1, respectively, on a 2.4 × 2.4 m spacing. Seedlings were planted in a sequential pattern, with alternate rows of (1) black walnut, (2) northern red oak and white oak, (3) black walnut and black cherry, and (4) northern red oak and white oak. Mean stand density at study initiation was 1350 trees ha^{-1} and basal area was 7.7 m^2 ha^{-1}.

All plantations in this study were established using random, unimproved genetic sources from Indiana provenances. Also, a combination of mowing and herbicide was applied at time of planting as well as for the first few years after planting on all sites to reduce herbaceous competition. Fertilization was applied at site 1 for the first 6 years when corn was grown, but not at sites 2 and 3.

2.2. Experimental design and tree growth data

A total of 28 trees were used among the three study sites, with 20 black walnut, 4 northern red oak, and 4 white oak (Table 1). The tree was the experimental unit (replicate), and trees were nested within study sites. For each replicate, diameter at breast height (dbh, 1.3 m above ground) was measured using a diameter tape for each tree at the beginning and end of each growing season. To account for differences in initial tree size, we calculated a relative growth rate (Vanclay, 2006). Relative diameter growth represents the percent gain of a tree between two measurements (Eq. (1)):

$$\textit{Relative annual growth rate}\left(\%\ yr^{-1}\right) = \frac{\left(\frac{Growth}{Initial}\right)\times 100}{\textit{Number of growing seasons}} \quad (1)$$

where *Growth* is the cumulative diameter growth during the measurement period (in cm), and *Initial* is the initial diameter at breast height at

Table 1
Study site information. Abbreviations: DBH, diameter at breast height (1.3 m above ground).

Site	Reference	Location	Age	Site index age 50 (m)	Species	n	DBH (cm)	Total height (m)	Middle canopy height (m)
1	Gauthier and Jacobs (2009)	40°19′44″ N 86°42′35″ W	20	24	*Juglans nigra*	8	23.1	16.2	11.6
2	Gauthier and Jacobs (2010a)	40°23′09″ N 86°55′56″ W	14	21	*Juglans nigra*	8	14.1	9.4	7.5
3	Gauthier and Jacobs (2010b)	40°23′07″ N 86°56′13″ W	14	18	*Quercus rubra*	4	5.3	6.0	3.3
					Quercus alba	4	7.0	6.1	3.3
					Juglans nigra	4	7.7	6.7	3.3